

MALE SIZE VARIATION AND MATING SITE FIDELITY IN A POPULATION OF *HABROPODA DEPRESSA* FOWLER (HYMENOPTERA: ANTHOPHORIDAE)

JOHN F. BARTHELL¹ AND HOWELL V. DALY

Department of Environmental Science, Policy and Management,
University of California, Berkeley, California 94720

Abstract.—The relationship between size and mating site fidelity was studied in males of the anthophorid bee *Habropoda depressa* Fowler during a two year period. Males appear to separate into two groups that locate mates differently. One group patrols patches of ground where bees emerge from nests constructed during the previous year. These males appear able to detect females that have recently emerged from nests or that are about to do so. Large numbers of these patrolling males struggle for prolonged periods to gain access to mates, frequently forming clusters around newly emerged females. Another group of males patrols flowering plants, apparently in search of foraging females that did not mate at the nesting site. Bees marked from both groups showed fidelity to their respective mating sites during mark-recapture studies. The two groups of males also differed significantly in size, with those from the flower sites being smaller on average than nesting site males. In addition, males from mating clusters were larger than other patrolling males at nesting sites. These patterns of male mating behavior parallel those found in other protandrous bee and wasp species.

Key Words.—Insecta, Anthophoridae, *Habropoda depressa*, protandry, mate-location, nesting site, size

Protandrous mating systems are common among solitary bee and wasp species (Stephen et al. 1969, Evans & West-Eberhard 1970). Early in the flight season, large numbers of males relative to females can produce extraordinarily high levels of competition for mates. In some species, males that patrol nesting sites form characteristic mating clusters around newly emerged females (O'Neill & Evans 1983, Longair et al. 1987, O'Neill & Bjostad 1987). Among some anthophorid bee species, males patrol nesting sites for mates as well as using alternative methods of mate-location. *Centris pallida* Fox males form mating clusters as well as waiting for females at the periphery of nesting sites (Alcock 1976). Similar examples exist for species in the genera *Amegilla*, *Diadasia* and *Habropoda* (Gordon 1984, Houston 1991, Neff & Simpson 1992, Cane 1994). Here we report direct evidence of alternative mate-location strategies by males of the ground-nesting vernal bee *Habropoda depressa* Fowler.

MATERIALS AND METHODS

Site Descriptions.—The study was conducted during March and April of 1991–92 on the University of California at Berkeley campus. Specimens of *H. depressa* were originally described from this site by Fowler (1899). Males were commonly observed flying near nesting sites when most females had not yet emerged. They were also seen in flight near these sites at several flowering plant species. Each nesting site (NS) represented an active emergence and nesting location for *H. depressa* females. In 1991, a NS on one of the least developed regions of the

¹ Current Address: Department of Biology, University of Central Oklahoma, Edmond, Oklahoma 73034.

campus, a forested hillside known as Observatory Hill, was chosen for study. Male behavior at this site was compared with that at a similarly sized flower site (FS) of Indian hawthorn (*Raphiolepis indica* Lindley) located about 50 m away. In 1992, male behavior was compared between another pair of sites ($\approx 10\text{--}20$ m apart) further up the same hillside.

Mating Site Fidelity.—Male mating site fidelity was studied by capturing and marking males at each of the two sites during both years. On 9 Apr 1990, samples of 80 patrolling males were netted from swarms of males while walking through each site. Each captured bee was marked with enamel paint on the center of its thorax and color-coded according to capture site. To ensure that males were not acclimated to their capture site, sweep samples from one site were transferred to the other site after being marked, i.e., those sampled from the FS were transferred to the NS for release and those captured at the NS were released at the FS. The following day another 80 males were captured from each site. The number and color (if any) of captured males from each site were then tallied. All bees were captured, marked and released within the same three hour period of each day (11:45–14:45) when male patrolling activity was conspicuous. The above procedure was repeated 18–19 Mar 1992.

Size Variation.—Size variation was examined by comparing the mean size of male bees from each site during both years. Bees that had been captured on the second day of each mark-recapture period were used for this purpose. A total of 80 bees from each site was therefore measured during each year. Head capsule width was used as the size estimate, a measurement commonly used in other studies of hymenopteran size (O'Neill & Evans 1983, Daly 1983, Alcock 1989, Dodson & Yeates 1989, Mueller et al. 1992). Measurements were made with a dissection scope ($12\times$) equipped with an ocular micrometer. The resulting means and variances for each group of each year were then compared using *t*-tests (Sokal & Rohlf 1981).

Collections were also made at nesting sites where male mating clusters, groups of males surrounding virgin females, were commonly seen near emergence holes. Four males from one aggregation were collected on 10 Apr 1991 and another 13 males from four aggregations were collected during a 2.5 h period on 18 Mar 1992 for comparison with NS males. Observations of mating behavior were also made at various times during the study.

RESULTS

Behavioral Observations.—Males patrolled both nesting and flower sites. Males at the NS flew rapidly in zigzagging patterns just above the ground where females had begun nesting or were still emerging. Small groups of males were commonly seen hovering near the ground, often above an emergence hole. Occasionally one would land, enter the hole and emerge several seconds later to continue hovering in the area. A virgin female, buried under a layer of loose soil on 8 Mar 1992, was investigated by males in the area and she was eventually uncovered by one male that attempted to copulate with her.

During female emergence, clusters of struggling males (each surrounding a female) were commonly seen at the NS. These mating clusters continued for several minutes until one male remained. During these struggles, one male typically held himself over the female dorsum while other males attempted to remove him (Fig.

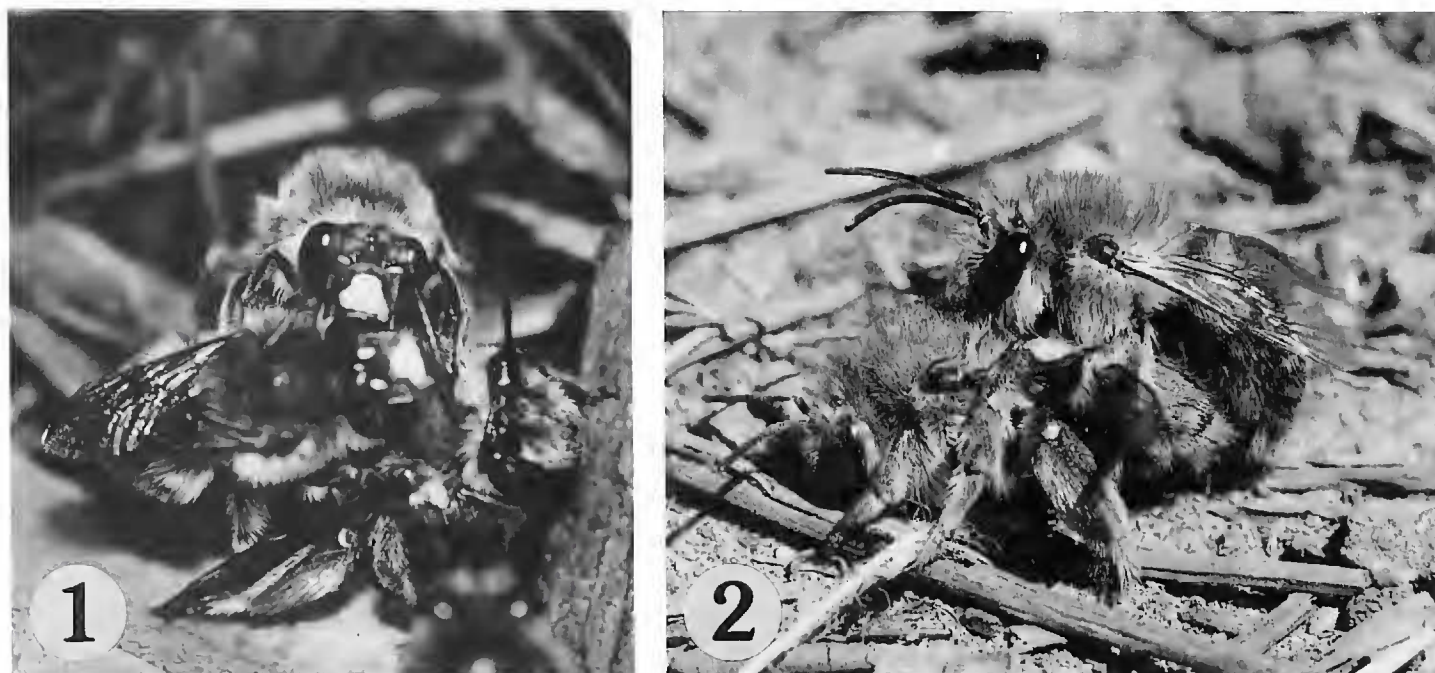


Figure 1. *Habropoda depressa* male attempting to dislodge another from a recently emerged female.

Figure 2. A mating pair of *Habropoda depressa*.

1). Presumably, the female at the center of a cluster had recently emerged from her nest cell because females that had initiated nesting were rarely approached by patrolling males. Similar, though smaller, groups of males were induced on 13 Apr 1991 at both the NS and FS by a tethered female that had been removed from a mating cluster while still attractive to males. The attractiveness of this female to males declined rapidly after the initial exposure to patrolling males. Brief contacts between males in the vicinity of mating clusters and nest holes were occasionally observed at nesting sites. It was unclear, however, if these interactions were aggressive, accidental or both.

Males and females were also commonly found foraging for nectar at the Indian hawthorn flower sites. Most males at these sites flew in erratic patterns over the surface of the hedges as well as at other flowering ornamental species including Chinese wisteria (*Wisteria sinensis* (Sims) Sweet), victorian box trees (*Pittosporum undulatum* Ventenat), an *Acacia* bush and a Japanese flowering cherry tree (*Prunus serrulata* Lindley). Unlike the NS, however, a mating attempt at flowers was observed only once when a male and female were found struggling on the ground under a victorian box tree directly below a group of patrolling males.

Attempted matings at the NS and FS were characterized by the same series of behavioral stages. Each began with the male securing a position over the female's dorsum. The male's front legs held the female between her front and middle legs while his hind legs were kept along the sides of her abdomen (Fig. 2). The female's wings were thereby pinned between his front legs and the female's thorax, preventing her from opening her wings. Once in this position, the male began a rhythmic opening, vibrating and then closing of his wings at regular intervals while moving his hind legs posteriorly and along the female's abdomen. The male's antennae were held straight during this process, often in alignment with the female's. When the abdominal apices of the female and male were nearly in contact, the male rapidly curled his antennae downward, while positioning his abdomen for copulation. Once in copula, the male twitched his antennae at regular intervals while the female remained mostly inactive.

Table 1. Numbers of male *Habropoda depressa* marked (Mrk) at respective mating sites and of those that were later recaptured (Rec). Contingency (2 × 2) test results from comparing actual and expected recapture numbers of bees that returned (Ret) or moved (Mov) to the other site are also presented.

Year	Flower site nos.				Nesting site nos.				
	Mrk	Rec	Ret	Mov	Mrk	Rec	Ret	Mov	
1991	80	4	3	1	80	16	15	1	$\chi^2 = 27.20, P < 0.001$
1992	80	6	5	1	80	5	4	1	$\chi^2 = 4.64, P < 0.050$

male twitched his antennae at regular intervals while the female remained mostly inactive.

Individual mating attempts varied slightly and did not always culminate in copulation. Many females resisted males by wriggling and moving their legs upward to disrupt the mating process or dislodge the male. One male was observed failing to copulate with a female despite six attempts to do so. All aborted attempts were attributed to female resistance. Intensity of resistance by females to copulation varied, and it was unclear whether this represented female mate choice or declining receptivity of females induced by previous matings.

Mating Site Fidelity.—Although few marked males were recaptured relative to all captured males for either the FS or NS groups during either year ($\leq 20\%$), recaptured (marked) males remained faithful to their original capture sites (Table 1). During 1991, for example, 16 marked bees were captured at the NS; 15 had returned and one had moved there from the FS. Four marked bees were found at the FS, three of which had returned there and one which had originated from the NS.

Similar results were obtained during 1992 although the distance between the NS and FS was shorter. Six and five marked males were collected at the FS and NS, respectively, and all but one had returned to the original capture site in each case. The recaptured males were not randomly distributed ($P < .05$) between the two sites during either year (Table 1), suggesting that they segregate into two mating groups: those that patrol female emergence sites and those that patrol flowering plants.

Size Variation.—The modes and means of male head capsule width samples were greater for the NS than for the FS for both years. The NS distributions (Fig. 3) are shifted to the right relative to the FS distributions. The two largest male size categories were found only in the NS and the smallest categories occurred only in the FS (Fig. 3a). Similar results were obtained in 1992 (Fig. 3b). Mean male head capsule widths were significantly larger in the NS for both years (Table 2).

Table 2. Mean head capsule widths for male *Habropoda depressa* collected at nesting and flower sites.

Year	Flower site			Nesting site			
	\bar{x}	(SD)	<i>n</i>	\bar{x}	(SD)	<i>n</i>	
1991	4.71	(0.12)	80	4.75	(0.10)	80	$t = 2.24, P < 0.05$
1992	4.75	(0.10)	80	4.79	(0.10)	80	$t = 2.54, P < 0.05$

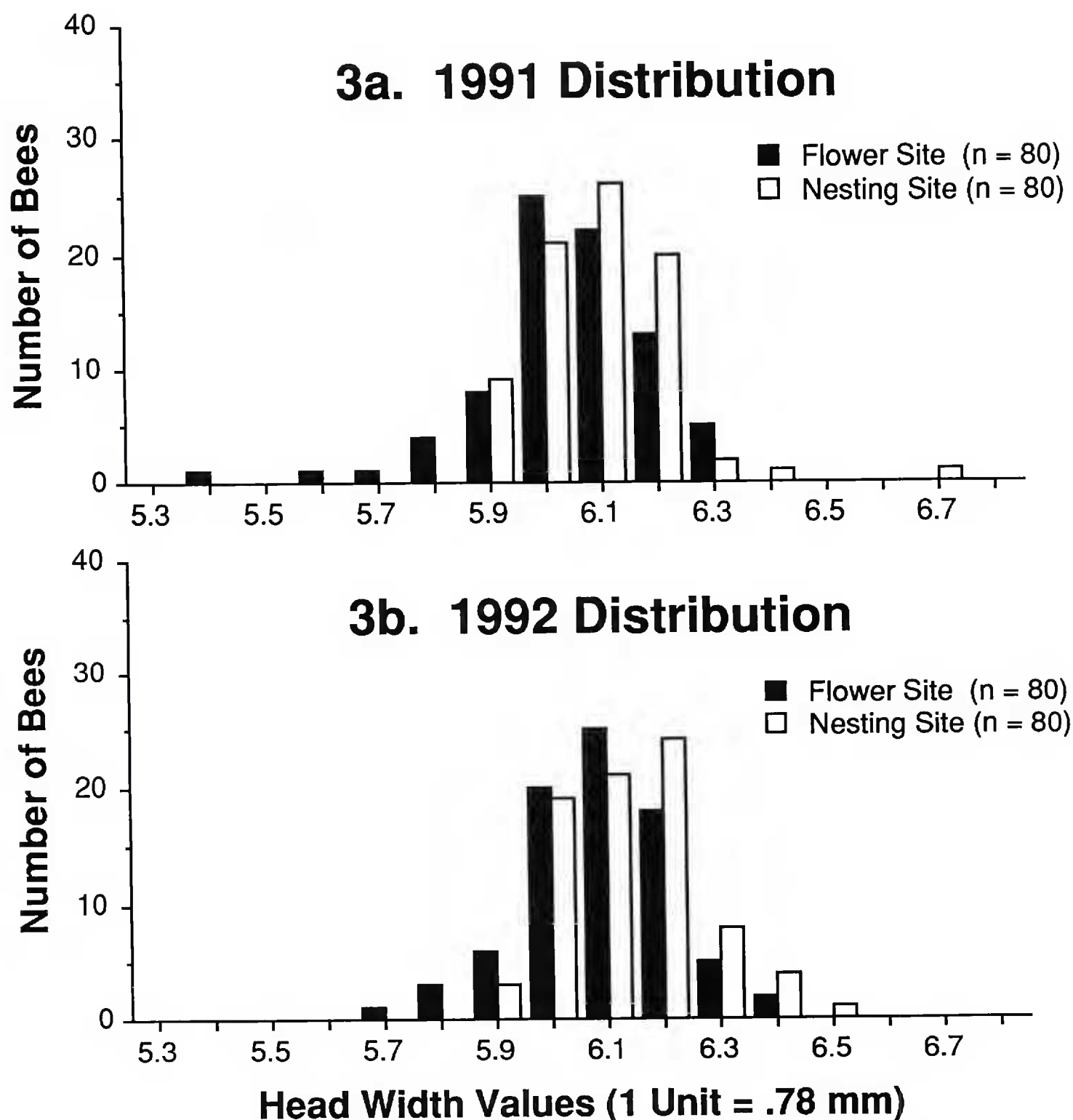


Figure 3. Distributions of head capsule widths for male *Habropoda depressa* collected from flower and nesting sites during 1991 (a) and 1992 (b).

The largest mean head capsule widths were recorded from males collected from mating clusters. The mean of four males taken from a single cluster in 1991 was significantly greater than NS males of the same year ($\bar{x} = 4.86$ mm; $t = 2.03$; $P < .05$). Similarly, the mean of 13 males taken from four mating clusters during 1992 was significantly greater than NS males of the same year ($\bar{x} = 4.88$ mm; $t = 2.97$; $P < .01$). The largest male collected during 1992 came from a mating aggregation and had a head capsule width of 5.14 mm.

DISCUSSION

Males of *H. depressa* employ at least two types of mate-locating behavior by patrolling either emergence sites or flowers to find receptive females. Males patrolling flowers are smaller than those at nesting sites. Although the exact mech-

anism for this size segregation is not known, evidence from this study suggests that intrasexual competition is important. Males attempt to pry one another away from females in mating aggregations. Less competitive (smaller) males are probably forced to peripheral sites such as trees and other flowering plants, thus increasing the average size of males in the NS.

The males found at flowers have a different mating strategy because direct competitive displacement probably does not occur at these sites. Rather, males rapidly responding to receptive females visiting flowers may have the most effective mating strategy. Smaller size may confer better flight maneuverability, an advantage to males trying to intercept females at flowers.

Mating success of FS males appeared low with one mating attempt observed during the study. This low mating frequency is not surprising as the many flowering plants on the campus and adjoining urban area produced numerous patrolling spots for males. The likelihood of a male encountering a foraging female was therefore low relative to the NS where females are concentrated at a few patches of ground. In addition, foraging females are presumably unreceptive to males because they were likely to have mated at the NS and had already begun constructing and provisioning their nests. The possibility remains that some females are not mated at the NS, however, and waiting for these females at foraging sites may therefore be a viable mating strategy for smaller males.

Alternative mating strategies may be widespread in the genus *Habropoda* (= *Emphoropsis*) (Brooks 1988). Gordon (1984) describes patrolling males and mating clusters in the beach-dwelling *H. miserabilis* (Cresson). Similar mating systems have been described for two other sand-nesting species, *H. laboriosa* (Fabr.) and *H. pallida* (Timberlake), including the occurrence of mating clusters (Bohart et al. 1972, Cane 1994). Timberlake (1962) also described evidence of male mating clusters in *Habropoda excellens* (Timberlake). In the case of *H. pallida*, some females were "unreceptive" to males, an apparent similarity to female resistance to mating described here for *H. depressa*.

The mating system of *H. depressa* resembles that described for species in other anthophorid genera, including *Amegilla*, *Centris* and *Diadasia*. Houston (1991) describes males of *Amegilla dawsoni* (Rayment) patrolling both nesting sites and flowering plants in Australia. Male size in this species conforms to a bimodal distribution and larger males appear to succeed most often at NS mating clusters while smaller males were most common at flower sites.

The mating behavior of *Diadasia rinconis* Cockerell closely parallels that of *H. depressa* (Neff & Simpson 1992). Males patrol both flower and nesting sites and male mating clusters were commonly observed at nesting sites, while less frequent matings were noted at flowers. Nesting females were not pursued by patrolling males, perhaps because previous matings had somehow rendered them unattractive. Guarding of sites containing potential mates was conspicuous among *D. rinconis* males though less pronounced among *H. depressa* males.

Male mating strategies in *H. depressa* also resemble those of *Centris pallida* Fox. Males of this species segregate into at least two groups, those that patrol nesting sites and those that patrol areas peripheral to nesting sites (Alcock 1976). Mating behavior is similar although olfaction appears to be more acute and mate-locating behavior less pronounced in *H. depressa*. *Habropoda depressa* males accurately located a buried virgin female and could apparently determine where

females would emerge, but were not observed excavating surface pits to meet emerging females as in *C. pallida* (Alcock et al. 1976). Rather, mate-location in *H. depressa* more closely resembled *D. rinconis* as both species investigate nest burrows but apparently without extensive excavation of unemerged females (Neff & Simpson 1992).

At least two hypotheses might explain the basis of mate-location described for the anthophorine genera *Amegilla*, *Centris*, *Diadasia* and *Habropoda*. First, as described for *C. pallida* (Alcock et al. 1977), the presence of numerous highly competitive males at discrete emergence sites (where females mate only once upon emergence) selects for male dimorphism. Such conditions exist for at least some species within each genus, although the intensity of male competition varies between and within species. Nesting sites on Santa Cruz Island (off the coast of southern California) generally appear less densely patrolled by *Habropoda* males than on the U.C. Berkeley campus (JBF, personal observation). Alternatively, then, it could be hypothesized that the less pronounced male dimorphism found in *H. depressa* may reflect a short-term effect of local competition, perhaps an ecological precursor to the extreme male dimorphism that may have evolved in *C. pallida* populations.

Identification of the proximate origin of size variation in *Habropoda*, *Amegilla* and *Diadasia* species would assist in discriminating between these hypotheses. Alcock et al. (1977) predicted, for example, that *C. pallida* females determine male progeny size by varying brood cell provisions. Unfortunately, *C. pallida* typically produces only one cell per nest, making this hypothesis difficult to test (Alcock 1979). Nonetheless, size variation of *C. pallida* males is over twice that described herein for *H. depressa* and is maintained over time within populations (Alcock 1989), suggesting variation is directly produced from female provisioning behavior and is therefore genetically based. Lower variation and less pronounced bimodality in size of males suggest that environmental factors may be sufficient to explain male dimorphism in *H. depressa*, including the availability of resources such as pollen, nectar and nesting sites.

Evidence from this study and others indicates that multiple mating systems induced by protandry may be more widespread than previously recognized in the Anthophoridae. Aspects of non-anthophorid bee mating strategies, including *Colletes cunicularius* (Colletidae), *Nomia nevadensis* (Halictidae) and *Perdita texana* (Andrenidae) resemble those of *H. depressa* as well (Cane & Tengö 1981, O'Neill & Bjostad 1987, Danforth & Neff 1992). One or more characteristics of the mating strategies of *H. depressa* are also known for sphecoid wasp species (O'Neill & Evans 1983, Longair et al. 1987, Martin & Martin 1990). How widespread multiple mating systems are in the Hymenoptera, however, and whether ecological and/or genetic factors mediate their occurrence are questions that await further study.

ACKNOWLEDGMENT

Deep appreciation is extended to those who provided observations and assistance in the field: K. M. Delate, D. A. Fruitt, M. A. Prentice and R. Stone. D. M. Bromberger pointed out male behavior at flowers and provided access to plant identifications. A. J. Slater and M. J. Hurlbert in Pest Management, Physical Plant Services, identified plants and conveyed observations they had made on the bees. A host of U.C. Berkeley staff and students who were onlookers during the project

were often helpful as well. The manuscript was read and improved by M. Dormond, G. W. Frankie, D. M. Gordon and R. W. Thorp.

LITERATURE CITED

- Alcock, J. 1976. The social organization of male populations of *Centris pallida* (Hymenoptera, Anthophoridae). *Psyche*, 83: 121–131.
- Alcock, J. 1979. The relation between female body size and provisioning behavior in the bee *Centris pallida* Fox (Hymenoptera: Anthophoridae). *J. Kansas Entomol. Soc.*, 52: 623–632.
- Alcock, J. 1989. Size variation in the anthophorid bee *Centris pallida*: new evidence on its long-term maintenance. *J. Kansas Entomol. Soc.*, 62: 484–489.
- Alcock, J., C. E. Jones & S. L. Buchmann. 1976. Location before emergence of the female bee, *Centris pallida*, by its male (Hymenoptera: Anthophoridae). *J. Zool.*, 179: 189–199.
- Alcock, J., C. E. Jones & S. L. Buchmann. 1977. Male mating strategies in the bee *Centris pallida* Fox (Anthophoridae: Hymenoptera). *Am. Nat.*, 111: 145–155.
- Bohart, G. E., P. F. Torchio, Y. Maeta & R. W. Rust. 1972. Notes on the biology of *Emphoropsis pallida* Timberlake. *J. Kansas Entomol. Soc.*, 45: 381–392.
- Brooks, R. W. 1988. Systematics and phylogeny of the anthophorine bees (Hymenoptera: Anthophoridae; Anthophorini). *Univ. Kansas Sci. Bull.*, 53: 436–575.
- Cane, J. H. 1994. Nesting biology and mating behavior of the southeastern blueberry bee, *Habropoda laboriosa* (Hymenoptera: Apoidea). *J. Kansas Entomol. Soc.*, 67: 236–241.
- Cane, J. H. & J. O. Tengö. 1981. Pheromonal cues direct mate-seeking behavior of male *Colletes cunicularius* (Hymenoptera: Colletidae). *J. Chem. Ecol.*, 7: 427–436.
- Daly, H. V. 1983. Taxonomy and ecology of Ceratinini of North Africa and the Iberian Peninsula (Hymenoptera: Apoidea). *Syst. Entomol.*, 8: 29–62.
- Danforth, B. N. & J. L. Neff. 1992. Male polymorphism and polyethism in *Perdita texana* (Hymenoptera: Andrenidae). *Ann. Entomol. Soc. Am.*, 85: 616–626.
- Dodson, G. N. & D. K. Yeates. 1989. Male *Bembix furcata* (Hymenoptera: Sphecidae) behavior on a hilltop in Queensland. *Pan-Pac. Entomol.*, 65: 172–176.
- Evans, H. E. & M. J. West-Eberhard. 1970. The wasps. University of Michigan Press, Ann Arbor.
- Fowler, C. 1899. The *Habropoda* and *Didasia* of California. *Can. Entomol.*, 31: 283–286.
- Gordon, D. M. 1984. Ecology of bees from coastal dunes, Humboldt County, California. M.A. Thesis, Humboldt State University, Arcata.
- Houston, T. F. 1991. Ecology and behaviour of the bee *Amegilla (Asaropoda) dawsoni* (Rayment) with notes on a related species (Hymenoptera: Anthophoridae). *Rec. West. Aust. Mus.*, 15: 591–609.
- Longair, R. W., J. H. Cane & L. Elliot. 1987. Male competition and mating aggregations of *Glenostictia satan* Gillasp (Hymenoptera: Sphecidae). *J. Kansas Entomol. Soc.*, 60: 264–272.
- Martin, W. F. & R. F. Martin. 1990. Reproduction of the sand wasps *Stictia signata* (L.) and *Bicyrtes variegata* (Olivier) (Hymenoptera: Sphecidae) on the Carribean coast of Quintana Roo, México. *Pan-Pacific Entomol.*, 66: 71–78.
- Mueller, U. G., A. F. Warneke, T. U. Grafe & P. R. Ode. 1992. Female size and nest defense in the digger wasp *Cerceris fumipennis* (Hymenoptera: Sphecidae: Philanthinae). *J. Kansas Entomol. Soc.*, 65: 44–52.
- Neff, J. L. & B. B. Simpson. 1992. Partial bivoltinism in a ground-nesting bee: the biology of *Diadasia rinconis* in Texas (Hymenoptera, Anthophoridae). *J. Kansas Entomol. Soc.*, 65: 377–392.
- O'Neill, K. M. & L. Bjostad. 1987. The male mating strategy of the bee *Nomia nevadensis* (Hymenoptera: Halictidae): leg structure and mate guarding. *Pan-Pac. Entomol.*, 63: 207–217.
- O'Neill, K. M. & H. E. Evans. 1983. Alternative male mating tactics in *Bembecinus quinquespinosus* (Hymenoptera: Sphecidae): correlations with size and color variation. *Behav. Ecol. Sociobiol.*, 14: 39–46.
- Sokal, R. & F. J. Rohlf. 1981. Biometry (2nd ed). W. H. Freeman and Co., San Francisco.
- Stephen, W. P., G. E. Bohart & P. F. Torchio. 1969. The biology and external morphology of bees. Agricultural Experiment Station, Oregon State University, Corvallis.
- Timberlake, P. H. 1962. An interesting new species of *Emphoropsis* from California (Hymenoptera, Anthophoridae). *Entomol. News*, 730: 36–38.